How the importance of survival estimates in estimating Whinchat population dynamics depends on the scale of migratory connectivity and site fidelity

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Die Populationsdynamik beim Braunkehlchen hängt vom Grad der Zugkonnektivität und der Ortstreue ab, wie bedeutsam ist dabei die Schätzung der Überlebensrate?

<< German Zusammenfassung >>

Summary

Accurate monitoring of whinchat population dynamics requires accurate estimates of breeding season survival and productivity, non-breeding survival and site fidelity (dispersal, immigration and emmigration). But monitoring of non-breeding survival between breeding seasons is confounded by the scale of site fidelity resulting in low estimates, and this will vary dependent on breeding success. Only one study (in progress) has measured true survival of whinchats on the wintering grounds (in Nigeria) where site fidelity is probably very high. Results from an ongoing geolocator tagging study also show only very large scale connectivity (at the scale of thousands of kilometres) between breeding and wintering populations. This means that annual survival rates measured at any point on the wintering ground probably average true breeding and migration survival for a large part of the breeding range, giving a representative true survival rate to use in calculating population dynamics. More importantly, if we have a measure of true average annual survival then we can calculate the proportion of adults that are dispersing and also the scale at which they disperse for breeding populations. Between winter survival rates for whinchats are the same for first year birds and adults suggesting that the ubiquitous lower survival rate of juveniles must arise between fledging and arrival at their wintering territory: therefore survival estimates for this period should be investigated. If survival immediately post-fledging or just before migration is variable then this will greatly affect local population dynamics, but once migration starts – the multiple routes and large scale connectivity - will mean populations over a large area will be affected to the same degree. If survival during first migration has declined substantially anywhere then many populations in the Palearctic will be affected. Average annual true survival for whinchats greater than about 4 months old, across much of Eastern Europe is greater than 50%: therefore it is it likely that local productivity or survival pre-migration determines an individual

population's dynamics, with the overall trajectory for the population being determined by the additive effect of first migration survival. However, further estimates of whinchat true annual survival are needed from other areas of Africa to determine if overwinter survival is always high: if not then this variation would negatively affect all Palearctic whinchat populations because of large scale connectivity, in the same way that first migration survival may do.

Introduction and objectives

The whinchat (*Saxicola rubetra*) is a passerine migrant that breeds throughout Europe and Western Asia and winters in sub-Saharan Africa, concentrated primarily south of the Sahel in West Africa and in eastern central Africa (ELGOOD et al. 1966, PEARSON 1972, CRAMP 1988, DEJAIFVE 1994, HAGEMEIJER & BLAIR 1997, URQUHART 2002, WERNHAM et al. 2002). Breeding populations have declined drastically in recent decades (CALLION et al. 1993, YEATMAN-BERTHELOT et al. 1995, BASTIAN & BASTIAN 1996), for example, with an overall population trend of -16% across Britain in both upland and lowland areas and declines of over 80% in some areas (GIBBONS et al. 1993, HENDERSON et al. 2004) and this has accelerated in recent years (HENDERSON et al. 2014). Whinchats are now of conservation concern throughout Europe (TUCKER et al. 1994) and are red-listed in some regions, and in others populations have completely disappeared (KELLER et al. 2001, BURFIELD et al. 2004).
Principle drivers of declines are loss of breeding habitats, specifically through agricultural intensification and earlier mowing, which causes direct mortality of both nests and adults, reduces food availability, foraging efficiency and fledgling success (MÜLLER et al. 2005, BRITSCHGI et al. 2006, GRÜEBLER et al. 2008, TOME & DENAC 2012). The role of non-breeding survival in these declines, however, is unclear because survival estimates are confounded by variable site fidelity. This paper explores how estimates of annual survival can inform our understanding of the population dynamics of Whinchats, even if declines are predominantly driven by factors operating on the breeding ground. It explores the problems of estimating survival from breeding studies and how the scale of connectivity and site fidelity are crucial to estimating accurate survival rates that we can use to understand local and global population dynamics of a widespread, generalist long distance migrant such as Whinchats.

Factors determining population dynamics in whinchats: the problem of site fidelity

Whinchat population dynamics, as with all migrants, arises because of breeding season survival and productivity, non-breeding survival and site fidelity or dispersal (NEWTON 2008). With accurate estimates of these parameters it is possible to model whether a population is stable or not, and identify the key factors that most affect this. There are many European studies of Whinchats on

the breeding ground (e.g. this Symposium proceedings), and we have good estimates of survival during the breeding season and overall productivity (i.e. number of chicks fledged and the number of nesting attempts per pair). There is however a real problem in estimating true survival rates because of the issue of site fidelity, and particularly because breeding success itself may fundamentally change the probability that a bird returns to a study area.

Survival rates are usually estimated by mark-recapture studies: in their simplest form they record the proportion of marked individuals that return to a study site the following year and this proportion is a measure of survival rate. The problem is that these methods cannot distinguish between absence at the site in the second year arising because of dispersal rather than mortality (RICKLEFS et al. 2011, ERGON & GARDNER 2013). All mark-recapture studies therefore estimate apparent survival – a minimum survival rate – with true survival being higher with an additive component from individuals that have moved outside the study area. This site fidelity, or dispersal, confounds all survival studies to a greater or lesser degree (e.g. CILIMBURG et al. 2002). Clearly it is spatially dependent – if you can monitor the entire range of a species, or frame your study at the scale of the upper limits to a species' dispersal – then your apparent survival will equal your true survival (ANDERS & MARSHALL 2005). Also you can model dispersal at a small, tractable scale and make assumptions that this applies over all scales and so adjust your apparent survival upwards with an estimate of those birds lost by dispersal (GILROY et al. 2012, ERGON & GARDNER 2013, SCHAUB & ROYLE 2013). But both of these approaches have their limitations because of the scale at which dispersal operates in birds and particularly migrant birds that already operate on a global scale. Even dispersal over distances between 1-10 km (SUTHERLAND et al. 2000), and this may be common for many migrants (GREENWOOD & HARVEY 1982, SANDERCOCK & JARAMILLO 2002, MIDDLETON et al. 2006, FOERSCHLER et al. 2010) rules out effective monitoring except in the largest and most well-funded studies, and even these will not be able to deal with dispersal at the 100 km scale which again is common for even resident species (TITTLER et al. 2009). Modelling dispersal on a larger scale on the basis of monitoring on a smaller scale can undoubtedly provide some of the answer but there is a strong suggestion that dispersal and site fidelity may be highly variable and dependent on age and experience (MIDDLETON et al. 2006, SERGIO et al. 2009, BERNARD et al. 2011), and most particularly context so even between years there may be completely different patterns (MATTHYSEN et al. 2005, SERRANO et al. 2008). In short, a statistical model of dispersal from one year or one site or one population is unlikely to be applicable beyond the study system and area it was developed and any statistical model fundamentally cannot ever parameterise dispersal at longer distances without empirical data.

Some breeding season studies have measured high apparent survival estimates suggesting high adult site fidelity at the scale of the study (e.g. WOLFE et al. 2014), but others the reverse (e.g. SHITIKOV et al. 2012). Almost all studies have shown only large scale or low site fidelity – i.e. high dispersal - for first year

birds, so that apparent survival estimates will always be much lower than true survival for this age class. In Whinchats this also applies (BASTIAN 1992) and may be particularly pronounced. A recent study has shown extremely low site fidelity in Whinchats with return rates of adults being as low as 11% and for juveniles as low as 0% (SHITIKOV et al. 2015). Site fidelity between years is often a function of breeding success, with successful breeders being more likely to return the following year to the same site (SEDGWICK 2004, EEVA et al. 2008, SCHAUB & VON HIRSCHHEYDT 2009). This has also been shown to be the case in Whinchats, with adult apparent survival after successful breeding being 0.32 and after unsuccessful breeding 0.11 (SHITIKOV et al. 2015). This makes estimates of population dynamics even more complicated because a poor breeding season may lead to low apparent survival greatly exaggerating any population decline being measured (e.g. PAKANEN et al. 2011). In essence – because breeding site fidelity is dependent on breeding success, and breeding success will itself be related to probability of subsequent overwinter survival, or carry over effects from the previous winter - then it will inevitably be fundamentally flawed to attempt to estimate survival from return rates to the breeding ground.
Key to estimating true survival is then obtaining unbiased estimates of site fidelity or dispersal, or identifying stages in the life cycle where site fidelity is very high. The serial residency hypothesis (CRESSWELL 2014) suggests that for many if not all passerine migrants, winter site fidelity is likely to be very high. Migrants, because of the stochastic nature of how the arrive in Africa – at the scale of greater than 1000 km – are likely to be generalists in their habitat requirements and to be faithful to territories in the winter that promote survival (CRESSWELL 2014). Empirical evidence, although limited, suggests that several species have very high site fidelity on their wintering grounds (NEWTON 2008, see Table 2 in CRESSWELL 2014) and this is also the case for Whinchats. Here site fidelity has been found to probably operate at the smallest scale: if a whinchat is alive it returns to exactly the same site for at least part of the following winter (BLACKBURN & CRESSWELL 2015c). With very high site fidelity then true annual survival rates are fairly straightforward to estimate for Whinchats, all that is required is a colour-ringing study on their wintering grounds. The next problem then is how does an estimate of survival for any population in Africa relate to a particular breeding population in Europe: in other words what is the migratory connectivity between wintering and breeding populations in Europe?

Survival rates calculated on the winter quarters average many breeding populations because of large scale connectivity

The serial residency hypothesis (CRESSWELL 2014) predicts that connectivity between European breeding populations and African wintering populations for passerine migrants is likely to be low, or in other words, to operate only at a large scale (>1000 km). There is much empirical evidence, particularly recently from geolocator studies, that this is true (see Table 1 in CRESSWELL 2014).

Unpublished data (CRESSWELL et al.) from an ongoing geolocator study of Whinchats from a population in Jos, Nigeria, show that individuals tagged within about 40 km^2 of West Africa may breed across approximately two million square kilometres in Europe (or 1/3 of the Whinchat's global range). This combined with the European based studies of other passerine migrant species (e.g. KRISTENSEN et al. 2013, LEMKE et al. 2013) strongly suggests that annual survival rates measured at any point on the wintering ground average true breeding and migration survival for a large part of the breeding range, giving a representative survival rate to use in calculating population dynamics. This combined with high site fidelity then means that true average annual survival rates for Whinchat across large areas of Europe can be obtained from the wintering ground.

This observation that true survival rates for Whinchats (and perhaps most European passerine migrants) across large areas of Europe are best measured on the wintering ground is illustrated in Figures 1-3. Two hypothetical breeding populations, A and B will differ in their true annual survival because of differences in their migration routes and wintering areas (Fig. 1). As these populations increasingly use the same wintering areas (i.e. have connectivity at an increasingly larger scale only) so any differences between survival probabilities will average out (Fig. 2). As site fidelity decreases on the breeding ground so apparent survival will decrease and any absolute differences caused by degree of connectivity will decrease (Figs. 2 & 3), but the effect of site fidelity on underestimating true survival is always likely to be biologically significant even if only a small percentage of a breeding population is not site faithful.

A key further observation that arises from this framework is that the average survival value obtained for a European population may depend entirely on where on the wintering ground Whinchats are sampled. If there is heterogeneity in survival across Africa then any point sample of survival on the wintering ground may not be representative. In other words, if overwinter survival is particularly good or poor in one African wintering area, and overwinter survival is a key component to annual survival, then the estimate from Africa will only be relevant to a small number of birds, although these birds will be part of many breeding populations spread over a large area of Europe. It is relatively straightforward, however, to sample different areas of Africa for Whinchat survival to determine the degree of heterogeneity and to estimate an average "African" annual survival rate that can then be applied to all populations in Europe. Studies of Whinchats in Africa suggest they are particularly generalist and survive well regardless of habitat (HULME & CRESSWELL 2012, BLACKBURN & CRESSWELL unpublished), and indeed the serial residency hypothesis predicts that overwinter survival rates are likely to be fairly uniform within habitat zones Africa (CRESSWELL 2014), so it seems likely that just a few more studies across Africa will allow us to conclude a robust annual survival rate applicable to most European populations.

These inferences all depend on the assumption that Whinchats are very highly site faithful on the wintering grounds. With respect to this it is very important to point out that this does not necessarily mean that Whinchats only occupy one

site during the whole of the winter. Unpublished geolocator data (CRESSWELL et al.) and the variable occupancy of winter territories at specific areas unrelated to annual survival probability (BLACKBURN & CRESSWELL 2015c) strongly suggests that Whinchats may occupy more than one and possibly several territories during the winter period for weeks at a time and these may be separated by tens or hundreds of kilometres. But if the sites are used in one winter, then it seems that they are used every winter: thus as long as mark recapture occurs during their period of residency at any one of their sites, then site fidelity will not confound the estimates of true survival. If Whinchats habitually use several sites on a relatively large spatial scale over the winter then this will further increase the scale of connectivity in the population and survival over the winter for any individual will be the average over the range of sites used. Thus even if there is heterogeneity in survival dependent on wintering territory, this will be averaged out because sampling at a single site in Africa may sample Whinchats wintering over a large area of Africa.
With high site fidelity, estimating the degree of connectivity between wintering and breeding populations is then absolutely key to our ability to accurately determine survival rates relevant to particular European breeding populations from estimates on the wintering ground. Connectivity arises in birds mainly probably because of large scale barriers and constraints to routes (BOHNING-GAESE et al. 1998, HENNINGSSON & ALERSTAM 2005). Therefore in the west of West Africa, there will be a greater proportion of Western European Whinchats simply because Western Europe is closer and more westerly wintering areas are not possible. This means that at the very large scale (i.e. East versus West Africa) there may well be differences in annual survival measured on the wintering grounds that reflect these differences in routes, presence of barriers and breeding origin of Whinchats. Connectivity could also vary dependent on temporal mechanisms. If, for example, more northerly populations migrate later then prevailing weather systems or availability of stop-over sites varies, so changing the direction of migration and general area in Africa that the population ends up in. Again sampling annual survival in several areas within Africa is needed plus a greater knowledge of whether the scale of connectivity varies for populations wintering across Africa.

Implications of a single average true annual survival rate for large areas of Europe

If we can estimate a true annual survival on the wintering grounds that is representative for any particular breeding population across a large area of Europe then there are a number of important issues that arise: we can begin to estimate dispersal rates and so determine the meta-population dynamics of Whinchats in Europe; we can begin to estimate the degree to which post-fledging and first migration survival dominates population dynamics and we can

draw sensible conclusions about why we see a Europe-wide decline in Whinchat populations.

Using the difference between annual true and apparent survival rate to estimate dispersal

If we have a measure of true average annual survival then we can calculate the proportion of adults that are dispersing and also the scale at which they disperse for breeding populations. It is usually obvious in studies whether there is low site fidelity: apparent survival rates are too low to sustain populations and adult : juvenile ratios sufficiently high to suggest high levels of immigration (e.g. SHITIKOV et al. 2015). Nevertheless estimating the exact degree of dispersal using a baseline annual true survival rate for the population has not been possible to date. The additional considerable benefit relative to the cost that a few more overwinter studies would provide, in terms of allowing us to estimate variation in site fidelity across European populations, suggests that wintering ground studies should be a priority.

Post fledging and first migration survival – a missing link?

If there is only very large scale connectivity then any differences in population dynamics between European populations that cannot be accounted for by productivity must be to do with survival rates of juveniles in their first few months and their first migration. True survival rates estimated on the wintering ground can only assessed for first year birds from about September onwards, after their arrival in sub-Saharan Africa. Between winter survival rates for whinchats may be the same for first year birds and adults: the only study that has examined this for Whinchats showed, with reasonable statistical power, almost identical survival rate (BLACKBURN & CRESSWELL 2015b). This suggests that the ubiquitous lower survival rate of juveniles, and this probably applies for all passerine migrants that also show much lower first year survival (e.g. SÆTHER 1989, DONOVAN et al. 1995, SÆTHER & BAKKE 2000), must arise between fledging and arrival at their wintering territory. One study to date has examined this, and found that in Barn Swallows (*Hirundo rustica*) it is the post-fledging period, not the first migration period that has significantly lower survival (GRÜEBLER et al. 2014). The exact timing of the period of lower survival is very significant. If survival immediately post-fledging or just before migration is variable then this will greatly affect local population dynamics. Effort must then be expended to determine these rates for each individual European breeding population (by radio-tracking fledglings) to determine whether these rates are significant. Steps to address local population declines would then be focussed on the specific breeding population. If survival is variable during first migration however, then the multiple routes and large scale connectivity will mean populations over a large area (thousands of kilometres) will be affected by the same average survival (see CRESSWELL 2014). Consequently, if survival during first migration has declined substantially anywhere then many populations in the Palearctic will

be affected in the same way as for the wintering ground (although perhaps on a smaller scale, i.e. hundreds of kilometres dependent on whether the key period is the first or a later migration step).

Average non-breeding survival and overall whinchat population declines
Although we lack the necessary data at this stage to conduct a Europe-wide analysis of population dynamics, we can hypothesise on the basis of the existing limited data to begin to draw conclusions as to why Whinchats are declining so profoundly across Europe. Average annual true survival for whinchats greater than 4 months old, across much of Eastern Europe is greater than 50% (BLACKBURN & CRESSWELL 2015b, CRESSWELL et al. unpublished geolocator data). This is based only on a single West African site so far, of course. But if this is representative of other areas of West Africa – and we believe that our study site has fairly degraded and so typical habitats available (HULME & CRESSWELL 2012, BLACKBURN & CRESSWELL 2015a) – then the reason for any Whinchat population variation in Eastern Europe must be due to factors affecting productivity on the breeding ground or survival pre- or on onset of migration. The overall population trajectory will also be determined by the additive effect of first migration survival which has not been measured to date, but this would apply to all breeding populations in exactly the same way as overwinter survival because the same large scale connectivity applies (CRESSWELL 2014).
This means that for any declining population of Whinchats in Eastern Europe, where is productivity of more than 2 chicks per pair (to offset 50% or so annual survival), then post-fledging survival and/or first migration survival must be the key factors driving the population decline. Post-fledging survival in the first few weeks is very poorly estimated for most passerine species, but where it has been estimated, it is very high and significant (COX et al. 2014) and this includes Whinchats (TOME & DENAC 2012). Survival during the first year, measured on the breeding ground, has never been estimated unconfounded by site fidelity, particularly because first year birds have much higher dispersal rates than adults (GREENWOOD & HARVEY 1982). If we did have a system where there was 100% site fidelity for juveniles (i.e. a very large scale or insular study, e.g. FOERSCHLER et al. 2010) then we could simply assume that survival during first migration was the difference between survival during the first 12 months minus survival measured from month 4 to month 16. Without tags that tell us remotely what proportion of tagged juveniles die (e.g. STRANDBERG et al. 2010) we will not be able to carry out this calculation because large scale connectivity means that we would need to monitor survival through mark-recapture at an impossible continental scale. Nevertheless, with an estimate of survival from 4 months being greater than 50% across the whole of Eastern Europe, then any population with high productivity that exceeds mortality, yet that is still declining, must indicate a problem with survival of juveniles in the first 4 months. Post-fledging survival before migration can be estimated from detailed field studies on the breeding ground (e.g. TOME & DENAC 2012) – and if this can be eliminated as the

significant period of high mortality – then we are only left with first migration as the period of high mortality.

The first migration is likely to be a major bottleneck for survival in passerine migrants (NEWTON 2008). This may arise because of the process of locating a suitable wintering area for passerine migrants appears to be stochastic on a large scale (CRESSWELL 2014). This stochasticity, however, makes evolutionary sense because migrants are generalists that have most likely evolved to deal with unpredictable environmental variation (CRESSWELL 2014). Climate change is one of the characteristics of Africa and rainfall patterns shift on a continental scale on a decadal basis resulting in large scale change in vegetation and habitat suitability across Africa (NICHOLSON 2001). Migrants seem to have evolved a strategy to deal with this climate change across Africa: in other words, migrants do not put all their eggs in one basket. Juveniles from the same brood may end up spread over thousands of kilometres of Africa. At least one individual in a brood is therefore likely to find suitable habitat and then it returns to that area if it survives because, clearly, the location found was suitable. This strategy makes a lot of sense if habitat suitability shifts backwards and forwards across Africa with climate change. If however, habitat suitability simply degrades across Africa because of anthropogenic effects such as deforestation, conversion to farmland and overgrazing, then the proportion of juveniles each year that encounter less suitable habitats will progressively increase, so decreasing survival on average during the first migration. We know average habitat suitability for migrants is degrading generally across Africa (VICKERY et al. 2014) because human populations are increasing, and indeed at some of the highest rates globally in West Africa (CLELAND 2013). We also know from large scale connectivity and the ideas outlined in Figure 1 that any population in Europe will be affected by the average survival rate across Africa. Any detrimental change, anywhere in Africa will therefore affect a large number of European populations.

This scenario, however, is perhaps more applicable to other wintering Palearctic migrant species that rely on more pristine, forested habitats, although the evidence is that some of these migrants can maintain reasonable densities even in highly anthropogenically modified habitats (WILSON & CRESSWELL 2006, STEVENS et al. 2010). But Whinchat are clearly on the far end of this continuum in that they may actually benefit from the anthropogenic changes occurring in Africa, particularly because they occur in high densities in intensive farmland and Guinea savannah which has been substantially deforested (HULME & CRESSWELL 2012). It seems unlikely that the majority of Whinchats that arrive in Africa for the first time are limited by the availability of overwinter habitat. Therefore, if first migration survival rates have decreased then this must be to do with staging in Europe. Climate change has affected Europe and North Africa, particularly with respect to late summer rainfall (e.g. GIANNAKOPOULOS et al. 2009) and this may impact on successful fattening before the barriers of the Mediterranean and the Sahara (SALEWSKI et al. 2013). Changes in survival during first migration as one of the mechanisms behind Europe-wide Whinchat declines

remains pure speculation however, and will remain so until we can monitor where and when juveniles die.

To conclude: we have only one estimate of true survival from the wintering ground. Its high value and its applicability across Eastern Europe suggests that local breeding productivity, or survival before first migration, are responsible for population variation. Further estimates of whinchat true annual survival are needed from other areas of Africa to determine if overwinter survival is always high: if not then this variation would negatively affect all Palearctic whinchat populations because of the large scale connectivity in the same way that first migration survival may do. Overall however, estimating true annual survival for the majority of Whinchat populations in Europe can be achieved by monitoring several populations on the wintering ground and simply averaging the survival rates. The many Whinchat workers in Europe need to devote some of their effort to the wintering ground.

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Figure Legends:

Figure 1: Diagram of the hypothetical populations of whinchats and their connectivity and site fidelity used as an example to illustrate the importance of connectivity and site fidelity to estimates of survival and understanding population dynamics in whinchats. Survival estimates calculated from monitoring on either the wintering ground – where we always assume very high site fidelity – or the breeding ground are percentages in black: true survival in normal text and apparent survival in italics. Survival rate differences for the populations arise because of differences in survival during migration (i.e. different routes) or during wintering (i.e. different quality habitats or areas), here set for A to be 40% and for B 60%. The top panel shows high connectivity and high site fidelity – there is no exchange of birds in either breeding or wintering areas: therefore all birds have the apparent annual survival that reflects the true survival of their populations. The middle panel shows low connectivity and high site fidelity – populations share wintering areas: birds in A and B have a true survival on the breeding grounds which is the average of A and B, i.e. 50%. Apparent survival is the same as true survival because of high site fidelity. The bottom panel shows what probably occurs in whinchats: low connectivity and low site fidelity – populations share wintering areas and change breeding areas: birds in A and B have a true survival which is the average of A and B as in the middle panel, but because of low breeding site fidelity where 50% of the population shifts from breeding in A to B or vice versa, apparent survival is 50% lower at 25%.

Figure 2: How connectivity affects estimates of true and apparent survival. Two populations at study site A and B have the same breeding period survival, but have true annual survival rates of 0.4 and 0.6 respectively, the difference caused by small scale connectivity so that the two populations have differences in migration route and wintering ground leading to the annual survival differences (see Figure 1). If 100% of birds return to their site of marking then true and apparent survival are the same (solid line). As connectivity decreases (i.e. whinchats winter over a wider area and more breeding populations mix on the wintering ground) so that up to a maximum of 50% of population A now winters in B, so true survival increases because a greater proportion of the population have the higher survival rate associated with B. With decreasing site fidelity (dashed lines) apparent survival rate decreases, with lower apparent survival with higher connectivity, although the effect of connectivity on apparent survival becomes smaller as site fidelity decreases.

Figure 3: How the difference in survival rate between two populations B minus A (60% and 40% true survival rate respectively, see Figure 1) changes with connectivity and site fidelity. True survival (solid line with 100% site fidelity) difference decreases to zero as populations A and B migrate and winter in increasingly the same areas and so have the same average survival rate. This difference is lower dependent on the degree of site fidelity: any value lower than 100% gives an apparent survival value, and the difference with respect to connectivity decreases as site fidelity decreases.

Figure 1:

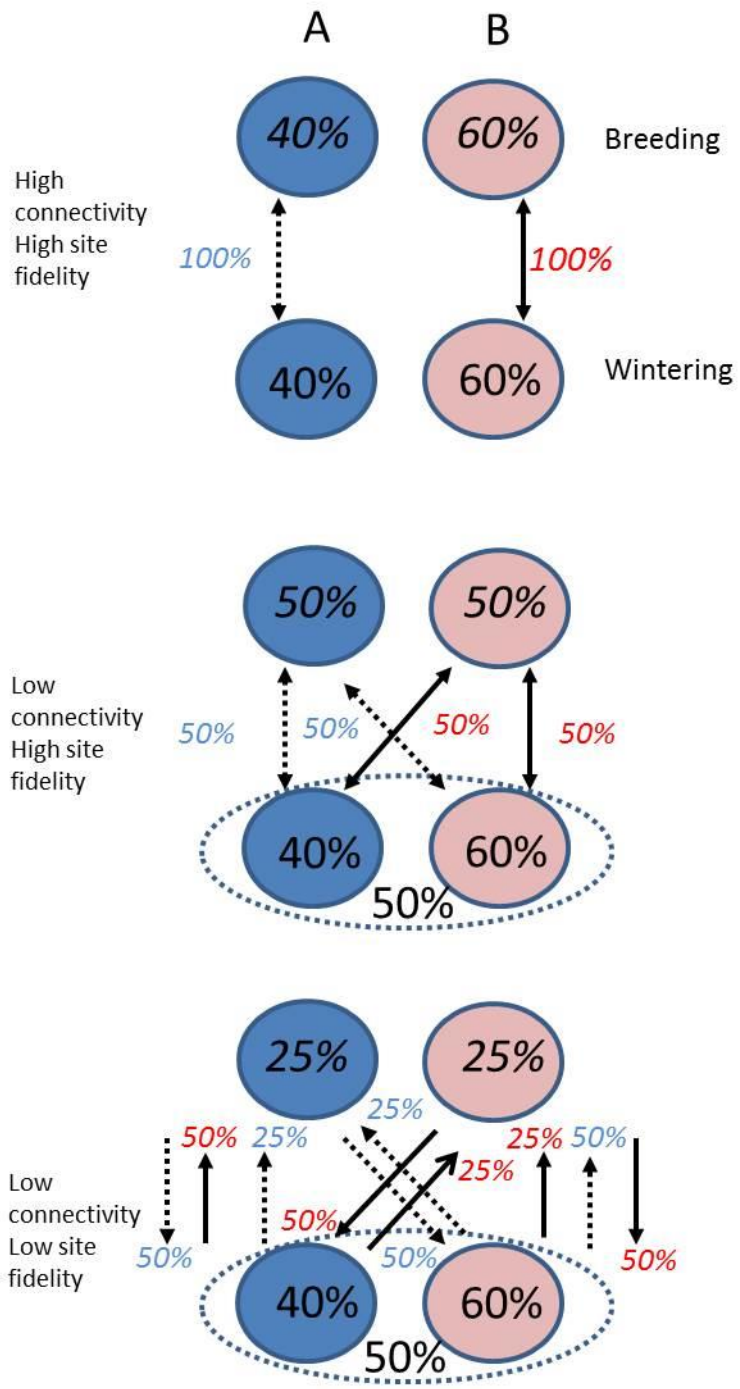

A
B
40%
60%
Breeding
High connectivity High site fidelity
100%
100%
40%
60%
Wintering
50%
50%
Low connectivity High site fidelity
50%
50%
50%
50%
40%
60%
50%
25%
25%
Low connectivity Low site fidelity
50%
25%
25%
25%
50%
25%
50%
50%
50%
50%
40%
60%
50%

Figure 2:

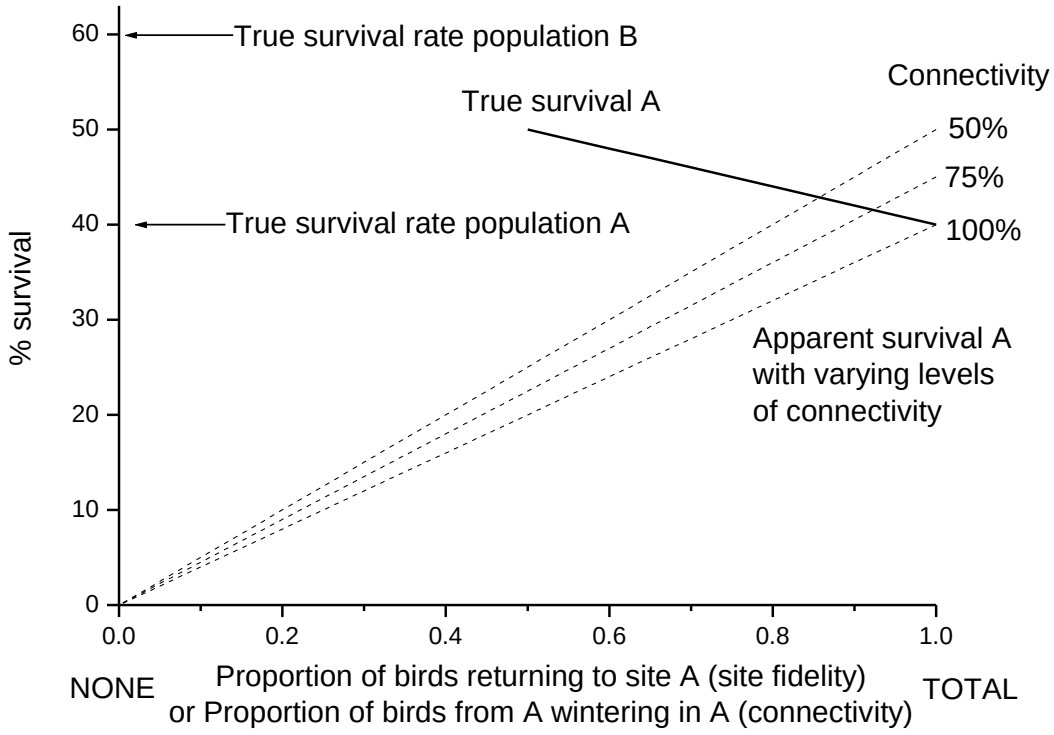
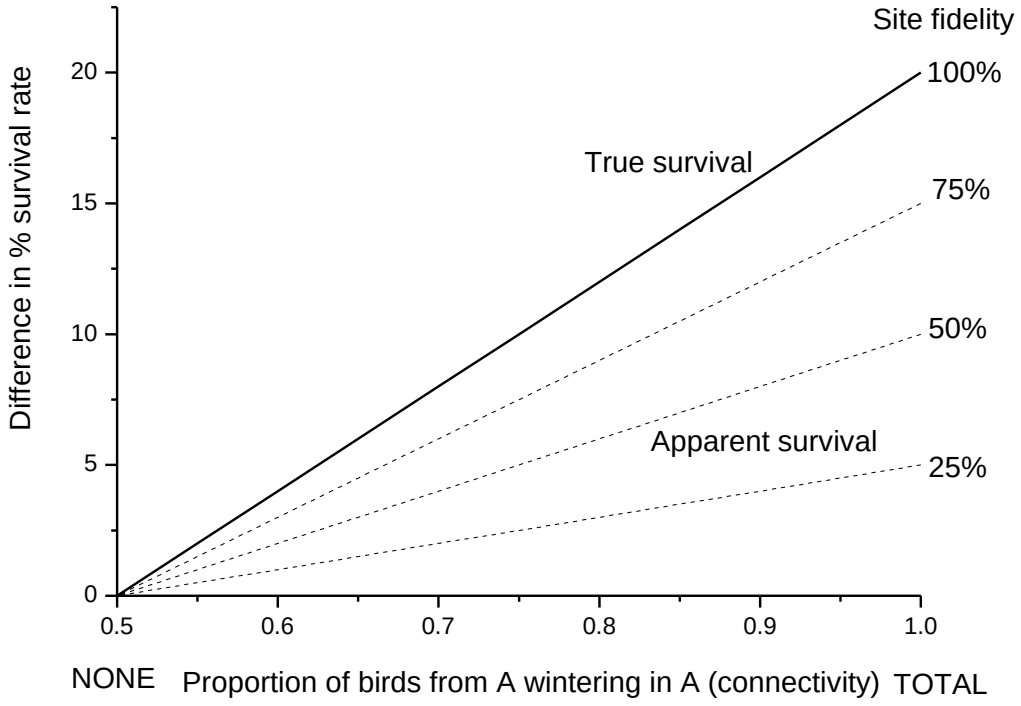

True survival rate population B
Connectivity
True survival A
50%
75%
100%
True survival rate population A
% survival
Apparent survival A
with varying levels
of connectivity
60
50
40
30
20
10
0
0.0
0.2
0.4
0.6
0.8
1.0
NONE
Proportion of birds returning to site A (site fidelity)
or Proportion of birds from A wintering in A (connectivity)
TOTAL

Figure 3:


Site fidelity
100%
75%
50%
25%
True survival
Apparent survival
Difference in % survival rate
0
5
10
15
20
0.5
0.6
0.7
0.8
0.9
1.0
NONE
Proportion of birds from A wintering in A (connectivity)
TOTAL